SEASONAL ABUNDANCE, HABITAT USE, AND DIET OF SHOREBIRDS IN ELKHORN SLOUGH, CALIFORNIA

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Large numbers of migrant and resident shorebirds feed and roost along the open coast, bays, sloughs, and marshes of California. However, more than 70% of coastal wetlands in California have been degraded by diking, filling, pollution, and other human activities (Speth 1979). Elkhorn Slough is one of the largest remaining salt marshes in California available to migratory shorebirds using the Pacific Flyway. Identification and conservation of critical habitats are required for an understanding of shorebird ecology and effective management of our resources (Senner and Howe 1984). Habitat use and foraging behavior vary from site to site (Baker and Baker 1973, Connors et al. 1979, Page et al. 1979), determined partially by the seasonal concurrence of shorebird movements and reproductive status, and habitat availability and preference. Abiotic factors (e.g., wind, tide, and temperature), as well as bird size and morphology, also influence distribution and behavior of shorebirds (Burger et al. 1977, Burger 1984).

Although some general patterns of shorebird distribution along the California coast are well documented (Jurek 1974, Shuford et al. 1989), trends in shorebirds' seasonal abundance and use of Elkhorn Slough wetlands are relatively unknown. Browning (1972) listed species, months of peak abundance, and maximum numbers of shorebirds in the slough. Seasonal occurrence and relative abundance of shorebirds in Elkhorn Slough were included in a broad census of California's wetland system, although observations were spatially and temporally limited (Jurek 1974).

Our objectives in this study were to describe the seasonal patterns in species composition and abundance of shorebirds in Elkhorn Slough, and to identify components of the ecosystem that support this assemblage. Use of habitat (intertidal mudflats, salt pond, and salt marsh) and feeding ecology of selected species were assessed.

Since 1983, more than 130 ha of diked wetlands have been returned to tidal action on the Elkhorn Slough National Estuarine Research Reserve. The salt ponds adjacent to the slough were exposed to tidal action in 1984. The present study, therefore, provides baseline information necessary for long-term monitoring of shorebirds in these newly restored marsh habitats.

STUDY AREA AND METHODS

Elkhorn Slough is a shallow tidal embayment and seasonal estuary on Monterey Bay (Figure 1), located about 160 km south of San Francisco, California. The slough has an axial length of 10 km and maximum width of 100 m at its mouth. The main channel is bordered by mudflats and is intersected by several small tidal creeks. Grain size of intertidal sediment decreases progressively from the mouth (82% sand particles >64 µm; 18% silt) to the most inland areas of the slough (67% clay and 33% silt; C. Jong, Univ. California, Santa Cruz, unpubl. data). During this study, water depth in the main channel below mean lower low water (MLLW) was 5 m at the

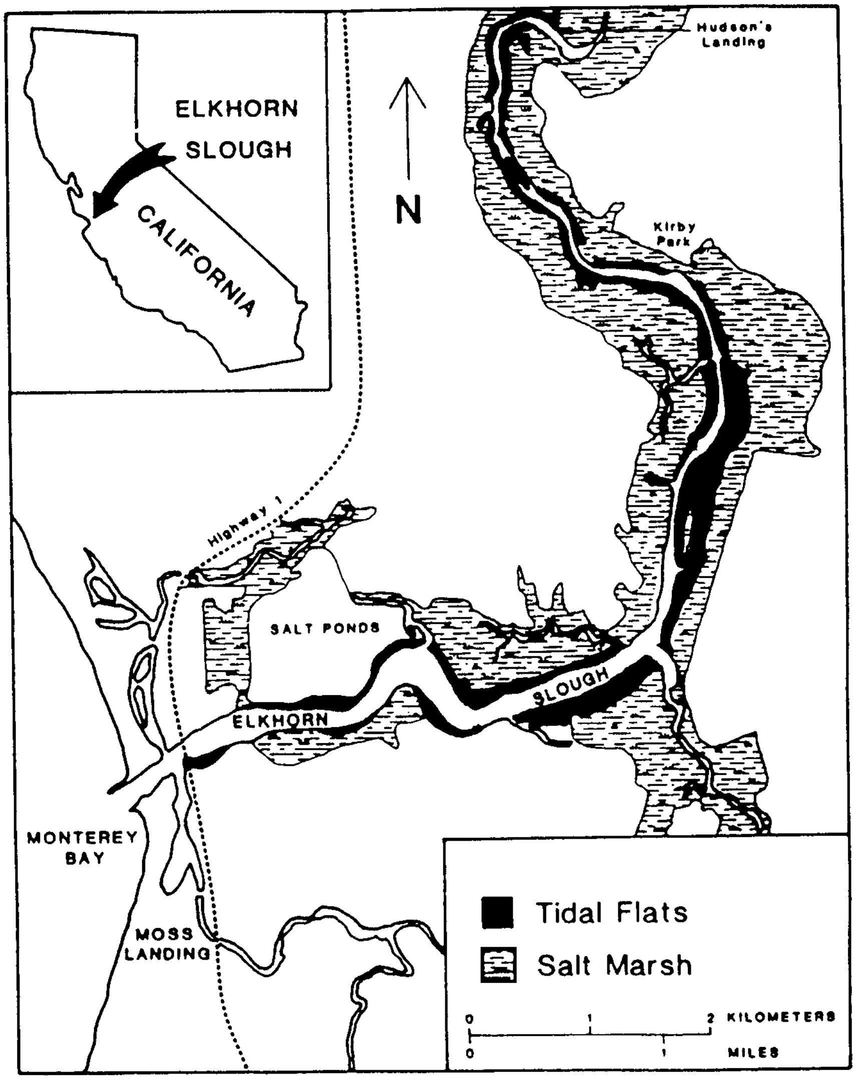


Figure 1. Shorebird survey area of Elkhorn Slough, indicating intertidal mudflats, salt marsh, and salt ponds.

mouth and <1 m at the most inland station; the mean tidal range was 1.1 m (Smith 1973, Broenkow 1977). About 170 ha of intertidal mudflats are exposed at MLLW (Browning 1972). Diked evaporating salt ponds (77 ha) are adjacent to Elkhorn Slough (Figure 1). An extensive salt marsh (583 ha) is located primarily on the northwest edge of the slough, and pickleweed (*Salicornia virginica*) is the dominant plant cover.

Surveys

We conducted our most intensive shorebird surveys from 1 November 1977 to 27 February 1980, along the main channel of Elkhorn Slough from California State Highway 1 to Hudson's Landing (Figure 1). At low tide, shorebirds on each intertidal mudflat and in adjacent salt marsh were identified and counted by one to four observers. Surveys were conducted from a small boat and lasted 1–4 hours. The direction of the survey route along the main channel and the state of the tides varied during each survey. All surveys were conducted between +1.2 and −0.1 m, relative to MLLW; mudflats were exposed within this range but the extent of exposure varied; see Ramer (1985) for tidal conditions during each survey. To minimize error associated with movement of birds among areas, we excluded any large flocks that likely were counted earlier. Number of shorebirds was converted to biomass by multiplying by the average weight of each species (Page et al. 1979) . Because of limited time at low tide, not all species were counted during every survey; abundance of common species, however, was determined at least once a month. Number of surveys during the year, therefore, is different for each species. Only surveys that included counts of all common species were used to estimate total and seasonal abundance of shorebirds.

To assess temporal patterns in abundance of shorebirds, we defined seasons as fall (July–October), winter (November–February), and spring (March–June). Summer was identified as the period (usually June) between the lowest abundance in spring and the increase in numbers in fall.

Habitat Use

Salt Ponds. To document shorebird use of salt ponds (Figure 1), we conducted additional surveys during October and November 1978. Numbers of birds roosting and feeding at five ponds were recorded over 3 hours on each of 12 days. Observations focused on the most abundant species: Western Sandpiper (*Calidris mauri*), Least Sandpiper (*C. minutilla*), and Dunlin (*C. alpina*).

Salt Marshes. We estimated relative frequency of roosting and feeding on 9 and 26 March 1979 for 10 minutes at 1-hour intervals in each of 3 hours during high tide at seven stations throughout the marsh (Figure 1).

Diet

From November 1978 to December 1979, stomach contents of Western Sandpipers (N = 25), Willets (*Catoptrophorus semipalmatus*; N = 21), and Marbled Godwits (*Limosa fedoa*; N = 24) were collected, primarily at one mudflat along the main channel of the slough. These were the most abundant species that represented a gradient in bill length and body size. Feeding birds were shot and stomachs were injected with 10% formalin in the field. Stomach contents of seven additional Western Sandpipers were collected by means of a stomach pump after feeding birds were trapped in a net in the salt ponds. Few prey items remained in the stomachs after pumping (Ramer 1985); this effective technique should be considered in place of sacrificing birds for future diet studies. All data on diet of Western Sandpipers were combined for analysis.

Prey parts were identified to the lowest possible taxon; number and relative volume (%) of each prey category in a stomach were estimated. Prey identification frequently was based on recognizable parts only, such as bivalve hinge fragments, amphipod uropods, and polychaete setae. A minimum prey number of 1 was assigned to taxon represented solely by parts (e.g., polychaete setae or pieces of algae). Prey categories in each stomach were ranked according to their index of relative importance (IRI; Pinkas et al. 1971), a function of relative frequency of occurrence (FO), relative number (N), and relative volume (V): IRI = $(N + V) \times (FO)$.

RESULTS

Seasonal Patterns

The most abundant shorebird species along the main channel of Elkhorn Slough were (in descending order) the Western Sandpiper, Dunlin, Least Sandpiper, dowitchers (Short-billed [*Limnodromus griseus*] and Long-billed [*L. scolopaceus*]), Marbled Godwit, American Avocet (*Recurvirostra americana*), Willet, Black-bellied Plover (*Pluvialis squatarola*), Long-billed Curlew (*Numenius americanus*), and Sanderling (*Calidris alba*). Other shorebirds occurred irregularly, and included a maximum of 46 Ruddy Turnstones (*Arenaria interpres*), 32 Semipalmated Plovers (*Charadrius semipalmatus*), 27 Whimbrels (*Numenius phaeopus*), 7 Greater Yellowlegs (*Tringa melanoleuca*), 6 Killdeers (*Charadrius vociferus*), 6 Red Knots (*Calidris canutus*), 3 Black-necked Stilts (*Himantopus mexicanus*), and 1 Lesser Yellowlegs (*Tringa flavipes*) per survey.

For the eight species common to each of 21 surveys along the main channel of Elkhorn Slough, total number increased during fall, from about 200 birds in June to 11,750 birds in November (Figure 2). From 6000 to 13,750 birds were counted during winter (the period of minimum migratory movement), and numbers decreased from spring to summer. Biomass similarly increased from 70 kg in June to 740 kg in November (Figure 2).

From counts combined by season over all years for each species, Western Sandpipers accounted for at least 75% of shorebirds present in every season (Figure 3). Numbers of each of the other species represented less than 10% of the total in any particular season. Small species (<150 grams body weight) made up at least 90% of the total number of shorebirds in all seasons (Figure 3). Total biomass was more evenly distributed between small and large (>150 grams body weight) species; one species predominated in each category. Western Sandpipers had the highest biomass of the small species, and Marbled Godwits had the highest numbers and biomass of the large species (Figure 3).

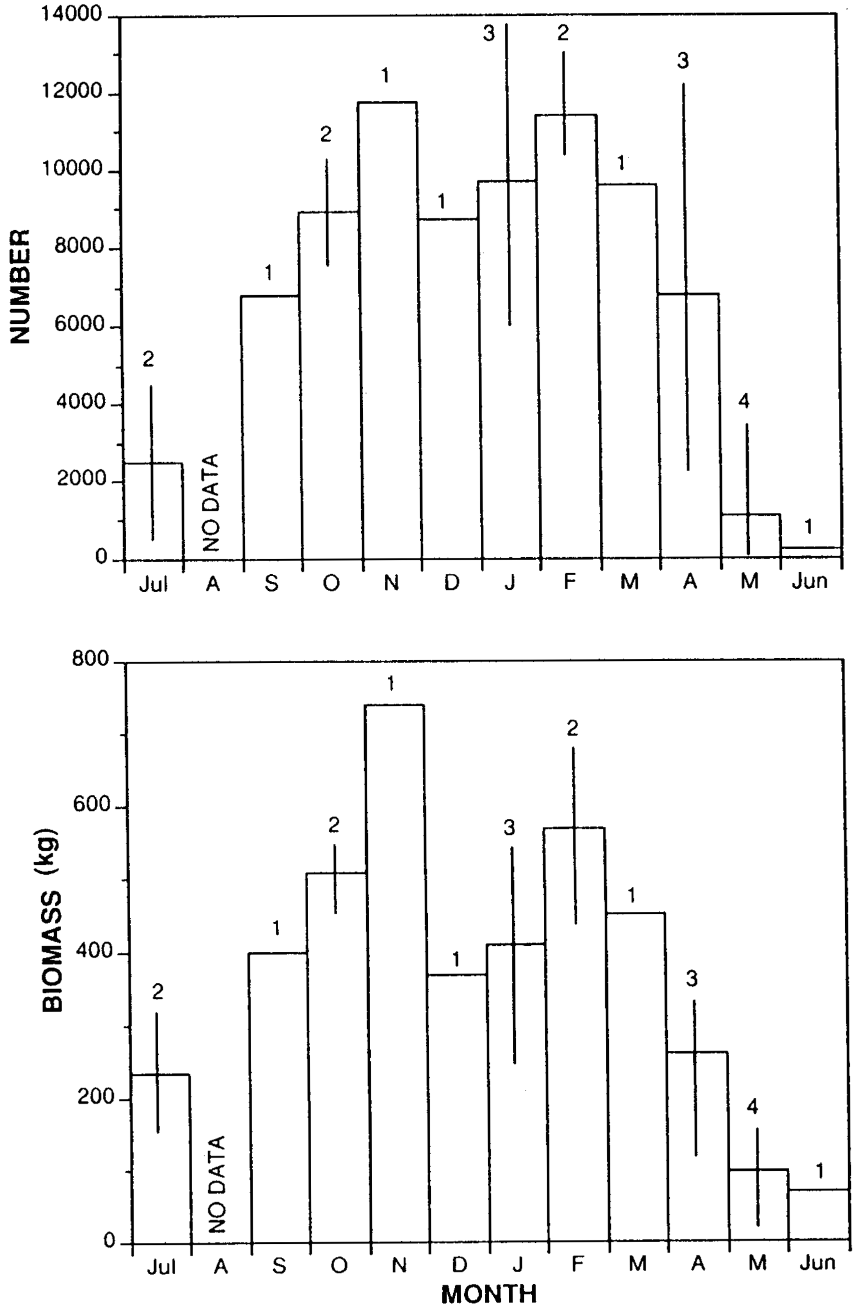
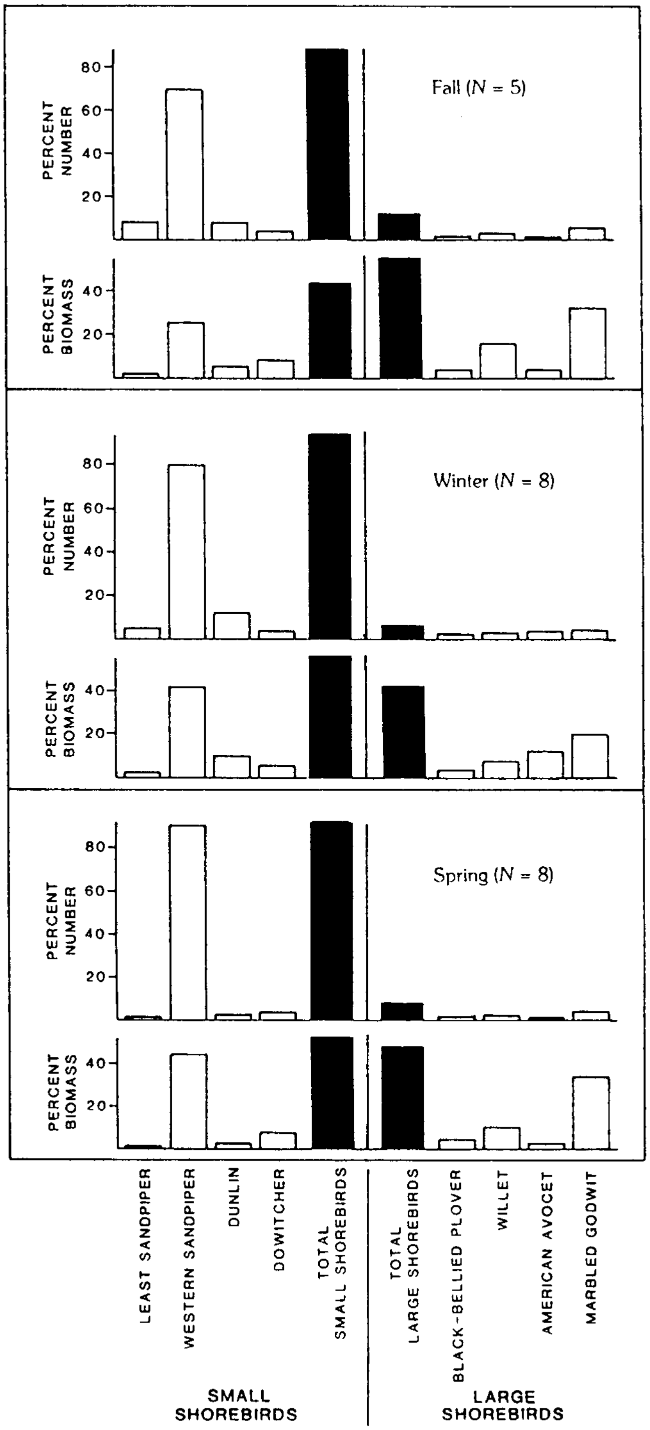


Figure 2. Seasonal changes in mean (vertical line is range) number and biomass of shorebirds along the main channel of Elkhorn Slough from November 1977 to February 1980. Number of surveys is indicated above each bar.


Fall (N = 5)
Winter (N = 8)
Spring (N = 8)
PERCENT NUMBER
PERCENT BIOMASS
80
60
40
20
LEAST SANDPIPER
WESTERN SANDPIPER
DUNLIN
DOWITCHER
TOTAL SMALL SHOREBIRDS
TOTAL LARGE SHOREBIRDS
BLACK-BELLIED PLOVER
WILLET
AMERICAN AVOCET
MARBLED GODWIT
SMALL SHOREBIRDS
LARGE SHOREBIRDS

The fall influx of most shorebirds began in June or July, except for that of Dunlins, which were not recorded until October (Figures 4 and 5). Least Sandpipers exhibited a fall peak in abundance, whereas Western Sandpipers did not (Figure 4). All common species overwintered in the slough. Numbers of Dunlins generally increased in early winter and spring. Although dowitchers were not distinguished morphologically, vocalizations indicated that more than 90% of the wintering birds were Long-billed Dowitchers. No small shorebird species were sighted in the area during summer, but nonbreeding birds of most large species were present during June (Figure 5). There was considerable variation in patterns of abundance for large and small species (Figures 4 and 5).

Habitat Use

Salt Ponds. Small shorebirds used the salt ponds primarily as a roost during high tide, secondarily as a feeding area. Western Sandpipers, Least Sandpipers, and Dunlins roosted in dense multi-species flocks in shallow ponds at the northwest corner and along dikes. From 830 to 20,730 small shorebirds (primarily Western Sandpipers and Dunlins) were counted per survey (N = 12) in the salt ponds. Of the small shorebird species that occurred in Elkhorn Slough, most individuals roosted in the salt ponds; no large flocks roosted elsewhere in the slough. Some small shorebirds fed intermittently near roosting flocks in the salt ponds. However, on average, 78.8% (standard error = 5.7) of Western Sandpipers and Dunlins were roosting. On falling tides, small sandpipers left salt-pond roosts and flew to exposed intertidal mudflats in the slough (N = 15 observations).

Large shorebirds also roosted in salt ponds. We observed as many as 350 Black-bellied Plovers and 700 American Avocets roosting in tight flocks in shallow ponds during single surveys. Willets and Marbled Godwits occasionally roosted in flocks up to 500 birds per survey, with only a few individuals feeding. Long-billed Curlews were not observed in salt ponds.

Several species fed in the salt ponds and were rarely or never observed in the main slough. We saw up to 400 Red-necked Phalaropes (*Phalaropus lobatus*), 200 Red Phalaropes (*P. fulicarius*), 150 Black-necked Stilts, 100 Snowy Plovers (*Charadrius alexandrinus*), and 30 Wilson's Phalaropes (*P. tricolor*) on single surveys. American Avocets, Black-necked Stilts, Snowy Plovers, and Killdeers bred locally in the salt ponds.

Salt Marshes. Maxima of 266 Willets, 257 Marbled Godwits, and 127 Long-billed Curlews were counted during the 3-hour surveys. These large shorebirds roosted and fed in salt marshes during high tides. Although most birds were observed flying over the marsh, an average of 24.3% (S.E. = 6.6) were roosting and 13.7% (S.E. = 4.2) were feeding. As the tide receded, most Marbled Godwits flew from the marsh to feed on intertidal mudflats. In

← Figure 3. Percent composition of most abundant small (<150 g) and large (>150 g) shorebird species by number and biomass from pooled data in fall (N = 5 surveys), winter (N = 8), and spring (N = 8) along the main channel of Elkhorn Slough. Species are ordered with increasing body weight from left to right.

contrast, some Willets and Long-billed Curlews continued to feed in the marsh during low tides. Some small shorebirds roosted on barren mudpans or in sparsely vegetated areas of marsh, but these scattered individuals never gathered in the large aggregations that occurred in the salt ponds. Small shorebirds never roosted in dense marsh vegetation.

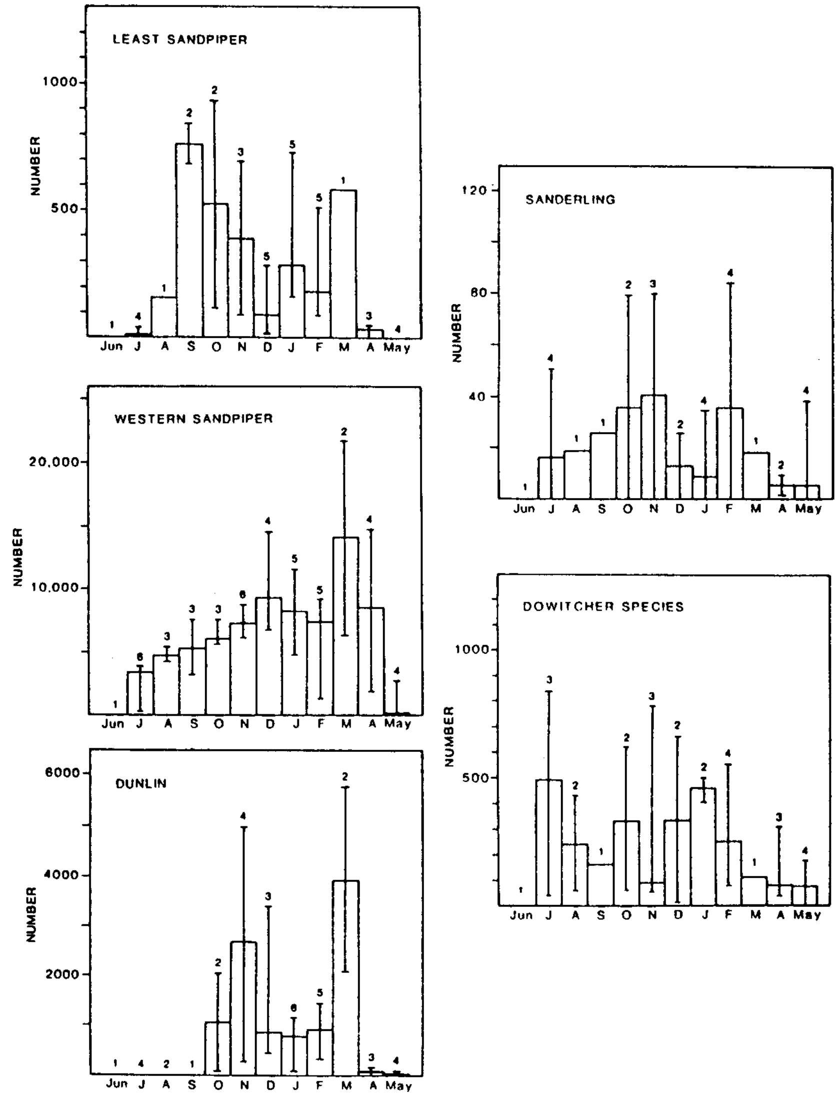


Figure 4. Median number (vertical line is range) of most abundant small (<150 g) shorebird species surveyed along the main channel of Elkhorn Slough. Number of surveys is indicated above each bar.

Mudflats. Intertidal mudflats were important feeding areas for all shorebird species. Density of Western Sandpipers that fed along the main channel of the slough increased generally with distance inland (the most muddy end of the slough), and was lowest at the most sandy intertidal flat near the mouth (Table 1). Mean densities of all large shorebird species were

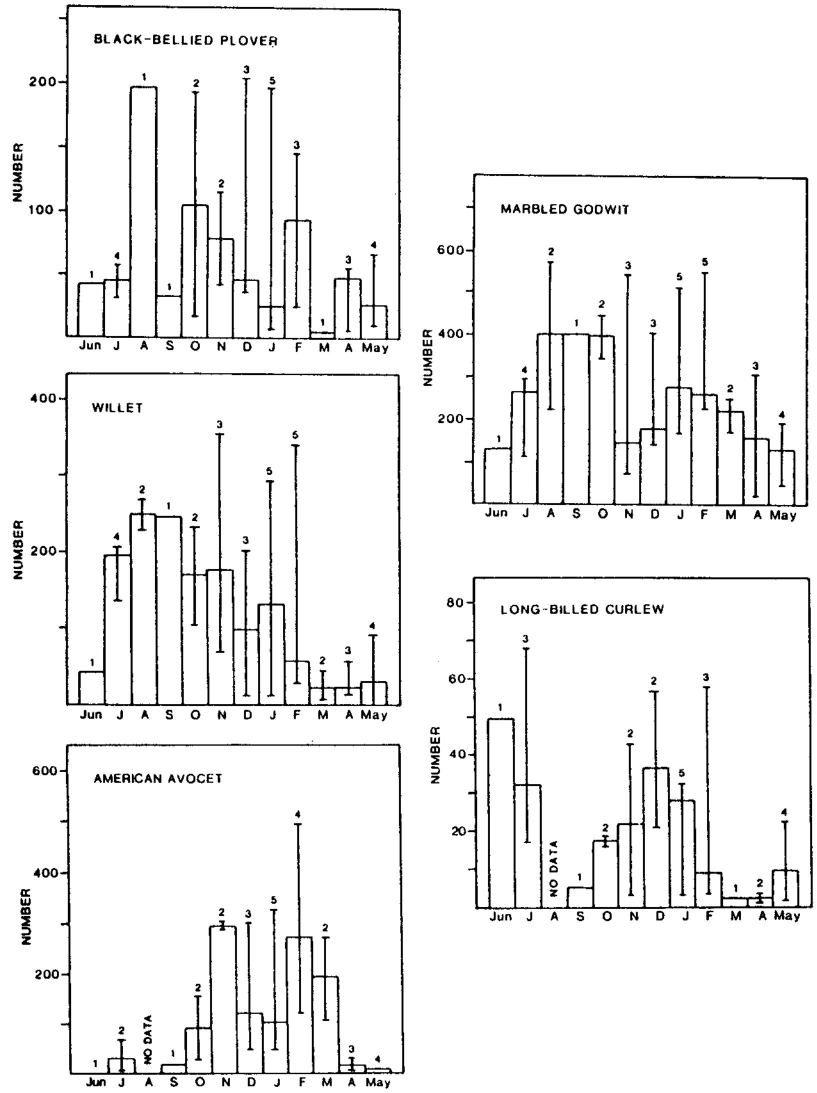


Figure 5. Median number (vertical line is range) of most abundant large (>150 g) shorebird species surveyed along the main channel of Elkhorn Slough. Number of surveys is indicated above each bar.

highest on mudflats about 3 km inland. Marbled Godwits and Sanderlings were the only species that fed in relatively high densities on the sandiest flats closest to the mouth. The relatively high mean density of Sanderlings at the most inland, muddy flat resulted from an unexpected count of 80 birds during one survey.

Diet

Western Sandpiper. Western Sandpipers primarily ate insects (mostly ephydrid fly larvae and pupae) and small infaunal invertebrates. Insect larvae and pupae ranked first in relative importance in fall and spring (Table 2). Prey composition of fall and winter samples differed markedly. Harpacticoid copepods, the bivalve *Gemma gemma*, Foraminifera, and the polychaete *Capitella capitata* occurred in at least 50% of stomachs from both seasons, but insects were not important in the winter diet (IRI = 11). Oligochaetes were found in 50% of the fall samples, but in none collected in

Table 1 Density (Number per Hectare) of Shorebirds Feeding on Intertidal Mudflats at Increasing Distance from the Mouth of Elkhorn Slough

	Distance up slough (km)				
Species	1	3	5	9	N^a
Small Shorebirds					
Least Sandpiper	0.7[b]	2.0	2.3	1.8	24
	(0.3)	(0.7)	(0.7)	(0.6)	
Western Sandpiper	5.5	51.6	100.6	64.4	24
	(1.6)	(8.5)	(14.8)	(13.0)	
Dunlin	4.4	7.1	13.2	10.5	19
	(2.4)	(2.3)	(6.7)	(4.3)	
Sanderling	0.7	0.1	0.1	0.2	14
	(0.2)	(0.1)	(0.1)	(0.2)	
Dowitcher	0.4	2.3	2.3	1.7	19
	(0.1)	(1.0)	(0.5)	(0.5)	
Large Shorebirds					
Black-bellied Plover	0.2	0.9	0.3	0.1	23
	(0.0)	0.3)	(0.1)	(0.0)	
Willet	0.4	1.4	1.2	0.6	22
	(0.1)	(0.4)	(0.3)	(0.1)	
American Avocet	0.3	2.1	1.0	0.5	16
	(0.2)	(0.7)	(0.3)	(0.2)	
Marbled Godwit	2.9	3.0	1.6	0.5	21
	(0.6)	(0.5)	(0.3)	(0.2)	
Long-billed Curlew	0.1	0.3	0.1	0.1	21
	(0.0)	(0.1)	(0.0)	(0.0)	

[a]Number of surveys.
[b]For each species, top row of figures is mean density, bottom row (in parentheses) is standard error.

winter. Amphipod crustaceans (*Corophium* spp. and Gammaridae) were the most important prey items in winter but nearly absent in fall. Although the relative occurrence of polychaetes (*Capitella capitata*) was high in fall and winter (FO = 75% and 86%, respectively), total number, volume, and IRI values probably were underestimated because of digestion (Page and Stenzel 1975, Quammen 1984). Algae, plant debris, and Foraminifera probably were ingested incidentally with other prey.

Willet. The highest-ranking prey of Willets in all seasons was the crab *Hemigrapsus oregonensis* (Table 3). In winter, another crab, *Pachygrapsus crassipes*, occurred in 63% of the stomachs, and ranked second in relative importance; crabs were the only prey in winter samples. In spring, Willets ate crabs and the opisthobranch snail *Haminoea*. Fall samples were more diverse, with eight prey categories. Willets ate many fewer species than did Western Sandpipers.

Marbled Godwit. In fall, polychaete worms (including *Capitella capitata*, *Boccardia hamata*, and Spionidae) ranked high in occurrence and relative importance (Table 4). Bivalves (*Gemma gemma* and *Macoma* spp.) also were relatively important (IRI = 942 and 412, respectively). In winter samples, these two bivalves were among the highest-ranking prey items. Polychaetes and crabs were secondarily important. No prey items occurred in more than 44% of the winter stomachs. In spring, the highest-ranked

Table 2 Seasonal Variation in the Diet of Western Sandpipers

	Fall (12)[a]		Winter (7)		Spring (11)	
Prey	%FO[b]	IRI[c]	%FO	IRI	%FO	IRI
Insect larvae	68	3063	14	11	100	15510
Seeds	68	2564	0	0	36	72
Harpacticoida	58	2115	57	237	0	0
Gemma gemma	50	801	57	157	18	119
Insect debris	42	627	43	293	0	0
Foraminifera	50	618	86	983	9	2
Capitella capitata	75	337	86	183	0	0
Algae and plant debris	67	321	57	318	54	76
Oligochaeta (Tubificidae)	50	172	0	0	0	0
Spionidae	42	119	0	0	0	0
Corophium spp.	17	7	100	5911	0	0
Gammaridae	0	0	71	3328	0	0
Ostracoda	25	23	100	1666	45	191
Crustacean fragments	25	36	43	525	0	0
Cumella vulgaris	25	23	43	317	0	0
Polychaete setae	8	1	43	179	0	0
Allorchestes angusta	0	0	43	70	9	6

[a]Number of stomachs examined in parentheses.
[b]FO, frequency of occurrence.
[c]IRI, index of relative importance (see text).

Table 3 Seasonal Variation in the Diet of Willets[a]

Prey	Fall (5)		Winter (8)		Spring (8)	
	%FO	IRI	%FO	IRI	%FO	IRI
Hemigrapsus oregonensis	40	855	88	9620	63	7201
Crab fragments	20	801	38	331	13	131
Orchestia traskiana	20	740	0	0	0	0
Hemigrapsus spp.	20	531	0	0	13	57
Eggs	20	389	0	0	0	0
Bivalvia	20	229	0	0	0	0
Algae and plant debris	20	219	0	0	13	181
Ostracoda	20	202	0	0	0	0
Pachygrapsus crassipes	0	0	63	3547	13	310
Haminoea/Bulla	0	0	0	0	13	129

[a]For abbreviations see Table 2.

prey categories were the crab *H. oregonensis* and the bivalve *Macoma* spp. Prey type, size, and diversity of the Marbled Godwit were intermediate between those of the Willet and the Western Sandpiper. Again, algae probably were eaten incidentally with other prey and occurred in the Marbled Godwit's diet throughout the year.

Table 4 Seasonal Variation in the Diet of Marbled Godwits[a]

Prey	Fall (6)		Winter (9)		Spring (9)	
	%FO	IRI	%FO	IRI	%FO	IRI
Polychaeta	83	5860	33	180	0	0
Capitella capitata	33	983	44	114	0	0
Gemma gemma	33	942	33	375	11	70
Spionidae	67	694	44	114	0	0
Macoma spp.	17	412	44	2248	44	1466
Bivalvia	17	211	33	776	22	301
Algae	50	115	33	599	67	1799
Boccardia hamata	17	95	6	0	0	0
Protothaca staminea	17	95	11	12	22	385
Macoma nasuta	0	0	44	1016	0	0
Hemigrapsus spp.	17	1	22	259	0	0
Hemigrapsus oregonensis	0	0	11	223	44	1926
Pachygrapsus crassipes	0	0	11	124	0	0
Crab fragments	17	16	0	0	22	675
Eggs	0	0	0	0	22	155

[a]For abbreviations see Table 2.

DISCUSSION

Relative to most coastal wetlands on the Pacific Flyway, Elkhorn Slough supports large numbers of wintering and migrating shorebirds, representing nearly 40 species (Point Reyes Bird Observatory [PRBO], unpubl. data). During recent surveys of 48 California wetlands that likely have more than 1000 shorebirds, Elkhorn Slough ranked third in gross number of birds, holding 1–3 % (>19,000 birds) of all shorebirds counted in spring and 5–6% (>30,000 birds) of those counted in fall (PRBO, Pacific Flyway Project, unpubl. data from September 1988 to April 1990). Comparison with Humboldt Bay, which ranked a close second in gross number of birds but which is 20–30 times larger in surface area, shows the importance of Elkhorn Slough to shorebirds along the central coast. Numbers of birds were highest (relative abundance 73-88%) in the San Francisco Bay system, whose surface area is several orders of magnitude larger than that of any other California wetland.

Shorebirds common in Elkhorn Slough occur commonly in other coastal wetlands along the California coast. As in Elkhorn Slough, either Willets or Marbled Godwits were among the most abundant large shorebirds, and Western Sandpipers, Least Sandpipers, dowitchers, and Dunlins were among the most abundant small shorebirds in San Diego Bay (Jehl and Craig 1970), San Francisco Bay (Page et al. 1990), wetlands from Point Reyes to Bodega Bay (Shuford et al. 1989), and Humboldt Bay (Gerstenberg 1979). The same large species that oversummer at Elkhorn Slough do so elsewhere along the California coast (Jurek 1974, Shuford et al. 1989).

There are some differences in abundance, however, between wetlands. Whereas Western Sandpipers clearly were the dominant species in Humboldt Bay, Elkhorn Slough, and San Francisco Bay, Least Sandpipers were as abundant in the Point Reyes area; Willets, Marbled Godwits, Least Sandpipers, and Western Sandpipers were equally abundant in Morro Bay (Stenzel et al. 1989, Page et al. 1990). Differences among wetlands in occurrence and relative abundance of shorebirds can be influenced by climate, hydrography, and habitat resources (Shuford et al. 1989).

Because species-specific density has not been estimated for shorebirds in most locations, comparisons among wetlands are difficult. Even though the most abundant wintering shorebird species were the same in Elkhorn Slough as from Point Reyes to Bodega Bay, densities in the slough usually were higher; e.g., mean densities of Western Sandpipers and American Avocets in the slough were about six times higher than maximum densities in the wetlands from Point Reyes to Bodega Bay (Table 5; Page et al. 1983).

Seasonal patterns in abundance of each shorebird species in Elkhorn Slough, as at any location, reflect time of migration and routes of travel between breeding and wintering grounds. In general, most species of wintering shorebirds move into California from July to November; spring exodus to the breeding grounds occurs from late March to early May (Jurek 1974, Shuford et al. 1989). In coastal wetlands of central California, peaks in abundance of fall migrants usually are apparent for Short-billed Dowitch-

Table 5 Mean Winter Density (Number per 100 ha) of Shorebirds on Tidal Flats in Elkhorn Slough and Range of Densities in Point Reyes–Bodega Bay Area

Species	Elkhorn Slough	Point Reyes–Bodega Area[a]
Least Sandpiper	213 (39)[b]	47–180
Western Sandpiper	6020 (490)	59–1055
Dunlin	1025 (243)	634–1299
Sanderling	23 (7)	16–129
Dowitcher (two species)	255 (63)	18–71
Black-bellied Plover	61 (14)	94–141
Willet	114 (23)	93–140
American Avocet	165 (28)	0–27
Marbled Godwit	223 (28)	113–758
Long-billed Curlew	20 (4)	0–12

[a]Includes Bolinas Lagoon, Limantour Estero, Drake's Estero, and Abbott's Lagoon. Data from Page et al. (1983).
[b]Figures in parentheses are standard errors.

ers, Least Sandpipers, Willets, Sanderlings, and sometimes Western Sandpipers and Black-bellied Plovers (Shuford et al. 1989). Marbled Godwits, Long-billed Curlews, American Avocets, and Dunlins do not exhibit these peaks. Spring peaks in abundance are described for Western Sandpipers and dowitchers. These general patterns in seasonal abundance do not apply to all the state's wetlands. For example, a well-defined peak was noted in fall for Western Sandpipers in Bolinas Lagoon, whereas very small or no peaks were obvious elsewhere around Point Reyes (Shuford et al. 1989).

The beginning of fall migration into Elkhorn Slough in July and spring movement out of the slough in late March generally follows the established migratory periods. Timing of fall migration is dependent on age and reproductive status of individual birds; e.g., generally, adults migrate earlier than do immature birds (Page et al. 1979). This extended migration can obscure peaks from site-specific surveys such as ours. Also, because dowitcher species were not distinguished in Elkhorn Slough, the larger population of wintering Long-billed Dowitchers could have masked the peaks of migrating Short-billed Dowitchers. A comprehensive survey of the regional wetlands of Monterey Bay, as well as a long-term intensive study of Elkhorn Slough, is necessary before seasonal patterns in abundance can be described adequately.

Changes in abundance also occur because of localized movements of shorebirds (Pienkowski and Evans 1984). Local movements may be synchronous with time lags between low tides at various locations, thus extending foraging time (Connors et al. 1981). Additionally, abundance can vary with daily movement of some species to feed in inland fields (Townshend 1981, Ruiz et al. 1989). Daily movements of Willets, Marbled Godwits, Black-bellied Plovers, and Sanderlings between Elkhorn Slough and adjacent beaches of the outer coast and river mouths occurred frequently during winter (J. Warriner pers. comm.). Irregular shifts in abundance of Least Sandpipers, Western Sandpipers, Dunlin, and dowitchers between the slough and the mouths of the Pajaro and Salinas rivers (5 and 8.8 km away, respectively) also are likely, because numbers of birds in these areas seem to fluctuate with habitat availability. Elkhorn Slough is the likely source of these birds because it is the closest large area of suitable habitat.

The restoration of wetlands in Elkhorn Slough resulted in increased surface area of mudflats and up to an average of 0.8 hours phase lag of high and low water relative to Monterey predicted tides (Wong 1989); these changes can influence shorebird foraging behavior and local movements. Movements of greater distance are possible, especially to San Francisco Bay, which because of its large size may serve to attract and aggregate shorebirds on the central California coast. Near Point Reyes, for example, Marbled Godwits and American Avocets move daily from foraging grounds in Bolinas Lagoon to probable nighttime roosts in San Francisco Bay (Blick 1980, Shuford et al. 1989). Snowy Plovers also move between Monterey and San Francisco bays (J. Warriner pers. comm.).

In Elkhorn Slough, shorebirds roosted in salt marshes and salt ponds during high tide, then moved to intertidal mudflats to feed at low tide. Shorebird species were not distributed evenly over tidal flats. The increased incidence of Western Sandpipers feeding at the most muddy intertidal sites in Elkhorn Slough recalls Quammen's (1982) findings that shallow-feeding shorebirds, such as Western Sandpipers, spent more time feeding and were more successful at prey capture on intertidal mudflats having little sand. She suggested that sand interferes with detection and capture of prey (small polychaetes and oligochaetes) because of similarity in size.

Seasonal changes in the diet of the Western Sandpiper and the Marbled Godwit were considerable, and probably related to spatial and temporal variation in availability of prey, although prey populations were not sampled. In other coastal wetlands, insect larvae and pupae (Order Diptera) occur in high densities near the surface of mudflats during warm fall months and are common in the diet of some species of small shorebirds, especially Western Sandpipers (Couch 1966, Page and Stenzel 1975, Stenzel et al. 1983). Other prey species of Western Sandpipers and Marbled Godwits were among the most abundant infaunal invertebrates in the mudflats of Elkhorn Slough (Nybakken and Jong 1977). Similar prey types have been reported in the diet of Western Sandpipers (Page and Stenzel 1975, Quammen 1984) and Marbled Godwits (Recher 1966, Holmberg 1975, Page and Stenzel 1975) from other coastal areas, although the relative importance of each type varied with location.

Salt marshes were used primarily by large shorebirds. Small shorebirds were not observed in areas of Elkhorn Slough where marsh vegetation was tall and dense, but they did feed and roost in sparse vegetation of the upper-slough marsh, suggesting that use of this habitat was restricted by height and density of vegetation. Willets were the only shorebirds that fed regularly in large numbers in the salt marsh. Their diet was dominated by crabs that are abundant in vertical banks of the marsh (Sliger 1982) and larger than the infaunal prey consumed by Western Sandpipers and Marbled Godwits on intertidal mudflats. Willets have similar feeding habits in other coastal wetlands (Reeder 1951, Recher 1966, Holmberg 1975, Stenzel et al. 1976).

The salt ponds adjacent to Elkhorn Slough were the primary roosting areas for small shorebirds, American Avocets, and Black-bellied Plovers. Salt ponds in San Francisco Bay were similarly used by these species (Swarth et al. 1982). Seasonal changes in water depth reduce space available for resting or feeding in salt ponds (Swarth et al. 1982); rising water levels from winter rains restricted this space for small sandpipers in Elkhorn Slough. In general, little feeding took place in the salt ponds, but there were important exceptions.

Several uncommon species of shorebirds (e.g., phalaropes) roosted and fed exclusively in salt ponds. The salt ponds were not flushed by the tide during our surveys. However, when a major dike broke in 1984 and a large salt pond was exposed to tidal action, many shorebirds began to feed on the new intertidal mudflat.

The considerable variation in spatial and temporal use of habitat by a large variety of shorebirds within Elkhorn Slough and surrounding areas, and exchange of birds between these habitats, suggests that this wetland system is important to the viability of migrating shorebird populations. The intertidal mudflats can be regarded as critical and sensitive habitat for many of the shorebirds feeding in Elkhorn Slough during their annual migratory cycle. Degradation of this habitat could reduce the reproductive success and affect the survival of these populations.

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